

SHORT COMMUNICATION

Sheet-web construction by *Melpomene* sp. (Araneae: Agelenidae)

Andrés Rojas: Escuela de Biología, Universidad de Costa Rica, Ciudad Universitaria Rodrigo Facio, San Pedro, San José, Costa Rica. E-mail: andresrova@gmail.com

Abstract. Sheet-webs are built by a variety of unrelated spiders. Some of these spiders are common, but information on their web construction behavior is scarce. This study describes the sheet-web construction behavior of *Melpomene* sp. (Agelenidae) and the sites where webs are built. I recorded the beginning of sheet-web construction by several spiders and analyzed photographs of webs in the field and the laboratory. Web construction consisted basically of two alternating behaviors: laying support threads and the filling in the sheet. These behaviors were repeated during several construction sessions until the available area was filled, or until the web reached approximately 80 cm². Apparently the spider uses both ampullate and aciniform lines for web construction, contrary to a recent description.

Keywords: Web building behavior, funnel web, ampullate lines, aciniform lines

Web building behavior in spiders provides useful characters for determining phylogenetic relationships due to its consistency and ease of observation (Eberhard 1982; Coddington 1986; Kuntner et al. 2008), and it is an important aspect of the biology of spiders due to the significance of the web in prey capture. There have been detailed studies of web-building behavior for a number of groups of spiders; however, information is very limited for spiders that build sheet-webs. Furthermore, sheet-weavers include species in distantly related groups of spiders, and their webs differ in structure and types of silk threads used (Grissold et al. 2005). It is very likely that the sheet-web construction behaviors vary among different groups of spiders.

Funnel-web spiders (Agelenidae) construct webs that consist of a flat sheet formed by dense layers of irregularly arranged silk lines near the ground. The sheet is connected to a funnel-shaped tunnel located at the edge or near the middle of the sheet. This tunnel serves as a place to eat, mate, hide and shelter egg sacs (Bristowe 1958; Foelix 1996; Matsumoto 2008). Some webs have threads above the sheet that may serve to intercept flying insects, causing them to fall onto the sheet (Ubick et al. 2005); the importance of this function, however, has not been demonstrated.

The family Agelenidae includes very common spiders like giant house spiders (*Tegenaria duellia*) Simon 1875 and common grass spiders (*Agelenopsis* sp.); nevertheless, details of the sheet-web construction behavior in this family remain unknown. This study provides a description of the sheet-web construction of the poorly studied spider *Melpomene* sp. (O. Pickard-Cambridge 1898) and observations about web placement in its natural environment.

METHODS

I observed the construction behavior of penultimate and antepenultimate females of *Melpomene* sp. collected in the Leonel Oviedo Reserve (1200 m elev.), Universidad de Costa Rica, San José, Costa Rica on April 6–June 30, 2009. Spiders were identified by Darrel Ubick in a previous study (Barrantes & Eberhard 2007). Several adult male and female voucher specimens are deposited in the Museo de Zoología, Universidad de Costa Rica.

Spiders were placed individually in 14 × 14 × 5 cm plastic boxes. The base of each box was covered with black cardboard, pierced by tacks. The tips of the tacks were 5 mm above the surface of the cardboard, and formed a grid with 1.5 cm between tacks. The tacks served as substrates on which the spider built its web, as well as reference points when analyzing the videotapes.

I analyzed the web building behavior of 12 spiders, seven of which had previously built a tunnel inside a twisted or rolled dry leaf. I

collected these seven spiders in the field by removing the web around the leaf while the spiders were inside and placed the leaf inside the plastic box. Five other spiders were placed in boxes with two or three dry leaves in which they had not previously made tunnels.

Once inside the boxes, spiders were kept in a dark room with a reverse 12:12 h L:D cycle to facilitate observation of these mainly nocturnal animals. Photographs of the web that had been built were taken every 24 h. The spiders were kept in captivity until the web occupied all available space, or until at least two days passed without further web enlargement (5–12 days). I sprayed the webs with water before taking pictures, in order to reveal the threads of the web. In the case of four randomly selected spiders, I recorded and analyzed the first 90 min of web construction (which began about 5 min after the spiders were placed in the box), using a Sony DCR TRV50 camera in night-shot mode. Because silk threads were not visible in the video recordings, I analyzed the behaviors performed by spiders and not thread placement. I made a diagram of time and behavior location on the plastic box for the spider that wove the largest web area, using Adobe Photoshop CS software. I also analyzed the time that the four spiders spent performing each behavior using JWatcher 1.0 software.

I took photographs of different random areas of one sheet web under a compound microscope to observe the lines placed as the result of each type of spider movement. I also took photographs of 20 sheet-webs in the field to measure their size and compare them with 12 webs built in captivity. I provide a brief description of the sites where spiders built their webs based on my observations while collecting the spiders.

Description of behavioral units.—The construction of the sheet-web consisted basically of three different behaviors: laying support threads, filling in the sheet, and resting /motionless.

Bee Line Movement (BLM): In this behavioral stage, the spider laid the support threads, generally walking fast (almost running) in a straight line without bending or tilting its abdomen, and keeping its posterior lateral spinnerets (PLS) directed posteriorly. Generally it moved in a radial direction from the tunnel or near it, to a substrate (tacks or container wall) beyond the edge of the sheet. When the spider reached the substrate, it flexed its abdomen laterally toward the substrate and paused briefly (0.7 s). During this time the threads were attached to the substrate, probably using the anterior lateral spinnerets. Then the spider returned along nearly the same path to the central part of sheet web or the tunnel.

Sheet Filling Movement (SFM): During this stage of web building behavior, the spider filled the sheet with fine silk. While

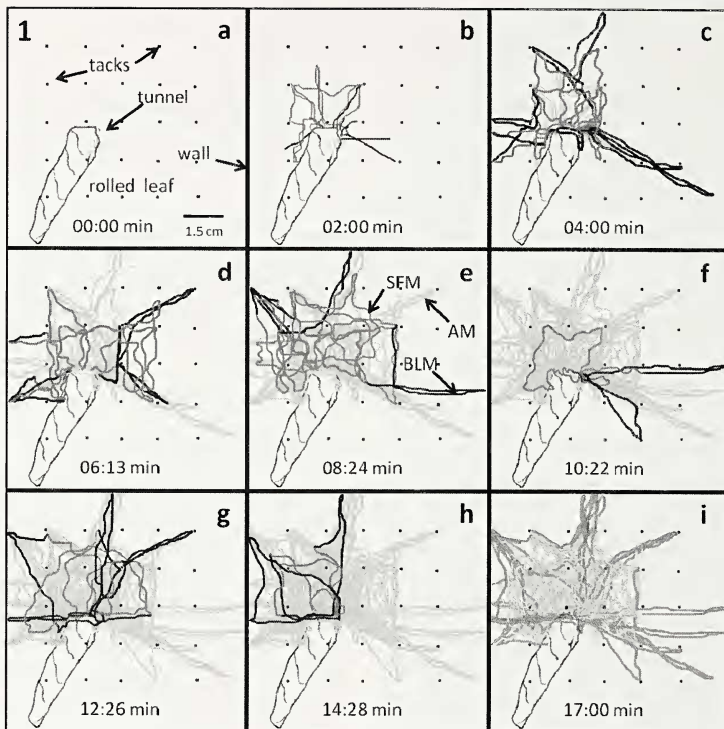


Figure 1.—Path of an individual *Melpomene* sp. during the first 90 min of sheet-web construction. Times shown in each figure indicate the net construction time. a) Before web construction; b-h) paths and types of movements during web construction, coded by color: BLM (Bee-line Movement) = Black, SFM (Sheet Filling Movement) = Dark gray, AM (Accumulated Movements) = Light gray; i) Accumulated construction movements in 90 min observed (darker lines = BLM and lighter lines = SFM). Between g) and h) were 22 min of inactivity; after i) the spider remained inactive.

filling the sheet, the spider walked rapidly, waving its abdomen from side to side repeatedly. Frequently, the PLS were open, forming approximately a 40° angle with the spider's longitudinal axis, while the spider walked and waved its abdomen. During the sheet filling, spiders followed an apparently erratic trajectory (Fig. 1).

Resting/motionless (RM): During this behavior, the spider remained motionless, mainly inside the tunnel or at its entrance.

RESULTS

In the field *Melpomene* sp. built their webs in the leaf litter, on the branches of shrubs, fallen trees and on the trunks of standing trees up to 2 m above the ground. It was common to find aggregations of up to 20 webs in an area as small as approximately 4 m². Webs built in the laboratory were similar to those built in the field.

All four spiders that I observed during initial web construction made the same three types of movements, but showed variation in their sequence. These behaviors often alternated (Figs. 1, 2), and their relative durations varied. The spiders repeated BLM many times, forming concentrations of radial threads that supported the sheet-web (Fig. 3b) and gave the exterior border of the web a polygonal shape

(Fig. 3a). At least two silk lines were produced during BLM, apparently by the anterior spinnerets (Fig. 3c).

Sometimes the spiders changed from BLM to SFM and vice versa without returning to the tunnel (Fig. 2). SFM occurred mainly in the central zone of the sheet (Fig. 1i) and probably resulted in the addition of multiple layers of silk.

In 1.5 h of web construction recorded, spiders used on average 7.1% (mean = 385 s, $n = 4$, SD = 223 s) in apparent thread placement; 40.6% ($n = 4$, SD = 7.8) of this time was spent performing BLM, and 59.4% of the time performing SFM. The rest of the time the spiders were motionless at the entrance or inside the tunnel (approximately 92.9%). During BLM and SFM, the spiders frequently returned to the tunnel entrance; normally they stayed away for approximately 10 s (SD = 14 s). I never observed thread manipulation with the spider legs.

Photographs of webs under the microscope showed at least two types of thread (Fig. 3d). The first type of thread was thick, and was always straight and oriented more or less toward the tunnel. Apparently these thick threads were placed during BLM. The second type of thread was more abundant, thin, often lax, and not oriented in consistent directions as the threads of the first type were. These

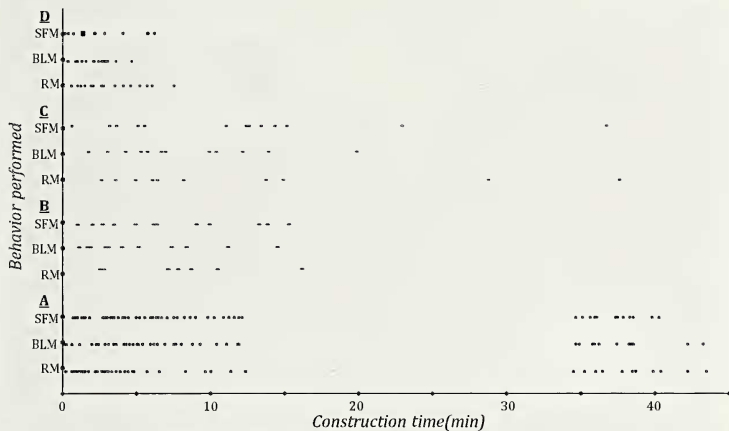


Figure 2.—Behaviors performed by four spiders during the beginning of sheet-web construction. (Spots show when behaviors initiate, not time spent during behaviors). Spider A was also used for Figures 1 and 4.

threads were presumably produced during SFM. I did not observe threads with balls of liquid on them.

Over several days the spider added new web to areas outside the original sheet (Fig. 4), and the sheet sloped more upward at the edges (Fig. 4d), due to the accumulation of attachment points on higher sites on the walls of the box. Areas that were built earlier gradually accumulated a thicker layer of silk. I did not find any order or pattern to where spiders added new web patches. The mean area of sheet-webs in the field was 808 cm² ($n = 20$, SD = 217 cm²), while that in the laboratory was 110 cm² ($n = 12$, SD = 75 cm²).

DISCUSSION

The sheet-webs built by *Melpomene* sp. consisted of an irregular, flat area with a tubular retreat. They were composed of non-sticky silk and suspended by silk threads attached at a few points to the substrate. The shape of the sheet web depended on the place of its construction, and the spiders added silk for several days to fill the available space (Blackledge *et al.* 2009).

At least during the first part of construction, and presumably during the remaining process, the construction behavior consisted of two types

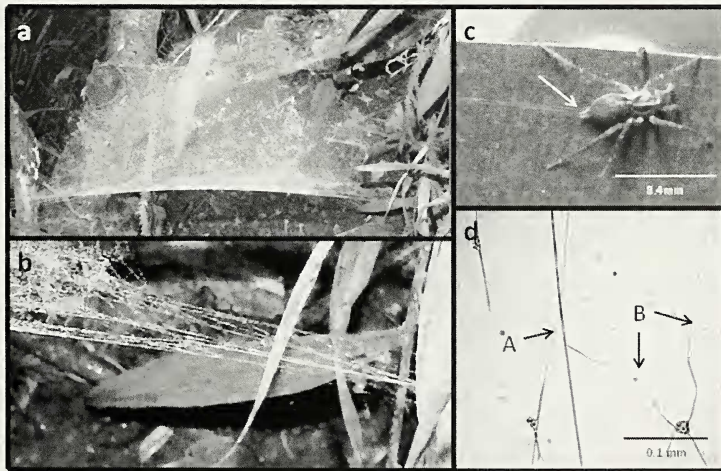


Figure 3.—a) Typical sheet-web of *Melpomene* sp. Note the tunnel in the central upper side. b) Concentration of radial threads that hold the web (detail of the lower right corner of a). c) *Melpomene* sp. during a Bee-line Movement (BLM). At least two threads were produced, and these apparently did not emerge from the posterior lateral spinnerets. d) Silk threads observed at the microscope, A thread probably produced during BLM, B thread probably produced during SFM.

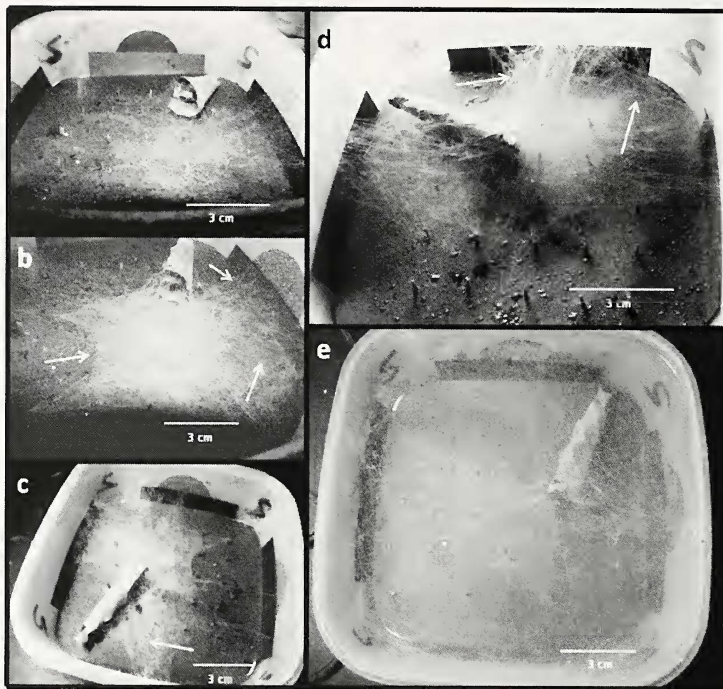


Figure 4.—Gradual development of a sheet web of *Melpomene* sp. a) day 2, b) day 3, c) day 4, d) day 7 (note the slope formation on the sides), e) day 10; finished web. Arrows indicate places where web area increased.

of behavior: placement of supporting threads and placement of filling threads. The support threads were probably produced by the ampullate spigots on the anterior spinnerets and laid during Bee-line Movements. Something similar occurs in *Neorania*, another agelenid spider that builds a web similar to that of *Melpomene* sp. (Griswold et al. 2005). Ampullate silk probably supports the rest of the web.

During sheet filling movements, the spider repeatedly waved its abdomen with its long posterior lateral spinnerets spread open, and the spider apparently left a swath of silk instead of a single pair of lines as it walked. Griswold et al. (2005) reported that surfaces of the sheet webs of *Eucragrus* (Dipluridae) and *Agelenopsis* (Agelenidae) result from the simultaneous action of many aciniform spigots located in the posterior lateral spinnerets. *Neorania* also has numerous identical spigots in its posterior lateral spinnerets (Griswold et al. 2005). If the arrangement of spigots on the spinnerets of *Neorania* sp. and *Melpomene* sp. are similar, then the silk laid during sheet filling movements by *Melpomene* sp. is probably also produced by aciniform glands. Unlike those reported by Griswold et al. (2005) in *Eucragrus* and *Agelenopsis*, and the report of Blackledge et al. (2009), the web of *Melpomene* sp. also has thicker threads, which has radial orientations.

Barrantes and Eberhard (2007) described how *Melpomene* sp. spreads its posterior lateral spinnerets while wrapping a prey, producing a greater coverage of the silk bands secreted by its long posterior lateral spinnerets. This same increase in coverage is probably also used by this species during the Sheet Filling Movement.

It is well known that when prey falls onto an agelenid sheet-web, the spider grabs it quickly and immediately returns with the prey in a straight line to the tunnel, even if the approach follows a tortuous path, which suggests that the spider uses different cues to calculate the direction toward the tunnel (Mittelstaedt 1985; Görner & Claas 1985; Barth 2002). This ability has been described for orb-web construction of *Leucauge mariana* (Tetragnathidae) (Taczanowski 1881) (Eberhard 1987). Probably similar orientation is important during sheet construction by *Melpomene*, as it continuously returned to the tunnel entrance, suggesting that it knew where it was located. Nonetheless, *Melpomene* sp. spiders might also use the ampullate threads as a cue to return to the tunnel, at least after the web is partially complete, since most have radial orientations. This feature could also be the parameter that the spider uses to obtain its approximate position in the web, though the wandering behavior of experimentally disoriented spiders argues otherwise (Görner & Claas 1985).

ACKNOWLEDGMENTS

I thank William G. Eberhard for useful comments on the experimental design and results. I also thank Anita Aisenberg, Ignacio Escalante, Gilberth Barrantes, Marianela Solís and Angel Solís. This research was supported by Escuela de Biología, Universidad de Costa Rica.

LITERATURE CITED

- Barrantes, G. & W.G. Eberhard. 2007. The evolution of prey-wrapping behaviour in spiders. *Journal of Natural History* 41:1631–1658.
- Barth, F.G. 2002. *A Spider's World: Senses and Behavior*. Springer-Verlag, Berlin.
- Blackledge, T.A., N. Scharff, J.A. Coddington, T. Szu, J.W. Wenzel, C.Y. Hayashi & I. Agnarsson. 2009. Reconstructing web evolution and spider diversification in the molecular era. *Proceedings of the National Academy of Sciences USA* 106:5229–5234.
- Bristowe, W.S. 1958. *The World of Spiders*. Collins, London.
- Coddington, J.A. 1986. Orb webs in non orb weaving ogrefaced spiders (Araneae: Deinopidae): a question of genealogy. *Cladistics* 2:53–67.
- Eberhard, W.G. 1982. Behavioral characters for the higher classification of orb-weaving spiders. *Evolution* 36:1067–1095.
- Eberhard, W.G. 1987. Memory of distances and directions moved as cues during temporary spiral construction in the spider *Leucage mariana* (Aranea: Araneidae). *Journal of Insect Behaviour* 1:51–66.
- Foelix, R.F. 1996. *Biology of Spiders*, Second edition. Oxford University Press, New York.
- Görner, P. & B. Claas. 1985. Homing behaviour and orientation in the funnel-web spider, *Agelena labyrinthica* Clerck. Pp. 275–296. *In* *Neurobiology of Arachnids*. (F.G. Barth, ed.). Springer-Verlag, Berlin.
- Griswold, C.E., M.G. Ramirez, J.A. Coddington & N.I. Platnick. 2005. Atlas of phylogenetic data for entelegyne spiders (Araneae: Araneomorphae: Entelegynae) with comments on their phylogeny. *Proceedings of the California Academy of Sciences* 56 (Supplement II):174–175.
- Kuntner, M., J.A. Coddington & G. Hormiga. 2008. Phylogeny of extant nephilid orb-weaving spiders (Aranea, Nephilidae): testing morphological and ethological homologies. *Cladistics* 24:174–217.
- Matsumoto, R. 2008. “Veils” against predators: modified web structure of a host spider induced by an Ichneumonid parasitoid, *Brachyzapus nikkoensis* (Uchida) (Hymenoptera). *Journal of Insect Behavior* 22:39–48.
- Mittelstaedt, H. 1985. Analytical cybernetics of spider navigation. Pp. 298–316. *In* *Neurobiology of Arachnids*. (F.G. Barth, ed.). Springer-Verlag, Berlin.
- Ubick, D., P. Paquin, P.E. Cushing & V. Roth. 2005. *Spiders of North America: an identification manual*. American Arachnology Society, Keene, New Hampshire.

Manuscript received 18 May 2011, revised 21 February 2011.